THE BREATHING AND FEEDING MECHANISM OF THE LAMPREYS. II.

(*Concluded.*)

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II. Food and Mechanism of Feeding.

A. *Mode of Attachment.* — If a living *Lampetra wilderi* or an *Ichthyomyzon concolor* (Kirtland) be placed in a glass dish its mode of attachment to the sides of the dish may be observed. The animal, when swimming freely, brings the sides of the oral funnel together so that it forms a vertical wedge-shaped cut-water which offers less resistance to the water than the open funnel. When it is about to attach itself, the closed funnel quickly opens against the glass and, with a single rapid backward and forward stroke of the tongue, the animal becomes firmly attached. The tongue in moving forward resumes its normal position in contact with the surface of attachment and is not seen to move again during the time of attachment, unless one attempts to pull the animal away in which case the tongue is seen to move as in the case of the first attachment. When the lamprey becomes accustomed to being handled it will seize one's finger and a strong suction may be felt resulting from the action of the tongue in the process of attachment.

If the oral funnel of a recently dead lamprey be pressed against the dish or finger, it becomes attached. If now one pulls the body backward in a direction at right angles to the surface of the attachment, it is found to be firmly attached. This attachment is so firm that one may lift from the water a dead lamprey thus adhering to the finger. If, instead of pulling the lamprey backward or away from the surface, one pushes it in any direction parallel to the plane of attachment, the oral funnel glides easily over the surface of attachment. When the lamprey is attached to a moving fish, the weight of the body as it drags through the water exerts a backward pull on the lamprey in spite of which the animal is able to maintain its hold, though at the same time it is free to glide in any direction over its host.

Since the dead lamprey remains attached, it is clear that the maintenance of the vacuum which effects the attachment is not through muscular action, but through mechanical means. Thus it is probable that the living lamprey may at times remain attached to the host without the expenditure of any muscular energy.

Is the vacuum by which the animal maintains its hold formed in the mouth cavity alone or in both mouth and pharynx? To determine this, the following experiments were tried on *Lampetra wilderi*. (1) A capillary glass tube was fitted over a cambric needle so as to form a small trocar. This was inserted into the nostril of a lamprey and so directed that the needle pierced the dorsal wall of the pharyngeal cavity. The needle was then withdrawn leaving the tube in the opening. The tube was occasionally cleaned by re-inserting the needle. The animal in which a communication was thus established between the pharyngeal cavity and the exterior was able to attach itself as firmly as before, thus showing that the vacuum is formed not in the pharynx but farther forward, *i. e.*, in the mouth cavity.

(2) A glass tube was inserted into the mouth cavity of a second lamprey between the lobes of the tongue. This tube was just long

enough to reach from the mouth opening to a point about 1 cm. back of the semiannularis muscle and establish a connection between the mouth cavity and that of the pharynx. At first the animal made fruitless attempts to attach itself and finally did so as firmly as ever. Upon examination, the animal was found to have swallowed the tube. A tube of the same length, but having a hook at one end, was now inserted into the mouth as before. The hooked end lay between the tongue lobes but did not interfere with the oral funnel in any way. It was found that the lamprey was neither able to swallow the tube nor to attach itself but lay on its side. Finally it was able to attach itself very feebly, but in order to do so the tongue worked back and forward continually, thus creating a slight vacuum.

(3) A guarded bristle was passed through the second external gill opening of a living lamprey into the water tube and on through the mouth so that the enlarged tip of the bristle lay between the tongue lobes, but did not interfere with the action of the funnel. The bristle thus prevented the complete closure of the velar valves and also the close approximation of the lateral tongue lobes. The animal was unable to attach itself except feebly by the aid of the continuous movement of the tongue already described. The bristle was drawn back of the semiannularis muscle so that it could no longer interfere with the action of the tongue, but was left where it would interfere with the action of the velar valves. The animal immediately regained the power to attach itself as firmly as before, thus showing that the velar valves do not aid in forming the vacuum in the mouth cavity.

From these experiments it follows that the partial vacuum which effects the attachment of the lamprey exists in the mouth and oral funnel only. The movement of the tongue at the moment when the animal attaches itself shows that the vacuum is produced at least in part by the pumping action of the tongue. The fact that after the animal has attached itself, the tongue projects forward, shows that the communication between the mouth cavity and the pharynx is not kept closed by the tongue, but probably by the semiannularis muscle, thus leaving the tongue free for other purposes.

In the case of the dead lamprey, the pumping action of the tongue must be replaced by the pressure exerted by the fingers against the oral funnel in the act of attaching the animal, the tongue then remains in the back part of the mouth cavity and thus functions in place of the semiannularis to close the communication between the mouth cavity and the pharynx.

B. *Mode of Feeding of Attached Lampreys.* — This has never been observed, nor is it likely to be, so that our knowledge of the process of feeding is an inference from the structures involved. The moment the animal attaches itself the oral funnel is opened quickly and is pressed flat against the supporting surface. The process may be watched when the lamprey attaches itself to the sides of a glass dish. The funnel may be so much flattened that the teeth on the tongue press against the glass.

In this position the teeth of the oral funnel and tongue constitute a very efficient rasping apparatus. Fürbringer (1875) has shown how the teeth of the funnel are moved in and out on radial lines by the action of the inner layer of the annularis muscle. The arrangement of teeth as already pointed out is such that in their movement along radial lines they necessarily lacerate every part of the surface covered by the funnel. It will be shown below that the tissues of the host are thus reduced to a fine pulp, which is then swallowed.

We may infer that this pulp finds its way into the pharyngeal cavity by the pumping action of the tongue. The considerable size of the pharnygeal cavity (Fig. 4) and the distensibility of its walls enable it to accommodate a large amount of food. By the contraction of the muscular wall, particularly the pharyngeus muscle and the basilaris muscles, the food is forced back into the œsophagus, while the posterior pharyngeus muscle relaxes to permit its passage.

C. *Character of Food.* — As regards the character of the food, there is much difference of opinion. Günther (1853) says: "Die Nahrung des Neunauges besteht ausser Würmern, Insekten, etc. noch in Fischen, sowohl kleinen, als grössern, an welche sie sich wie an Steine festsaugen." Günther does not indicate that he makes this statement from the examination of stomach contents of the lamprey, so that it is possibly merely a current belief.

Abbott (1875, p. 827), speaking of *Petromyzon marinus* says: "This fish which is found occasionally hibernating in the soft mud at the mouths of some of the inflowing creeks appears to come from the bay or ocean (at any rate from the lower portion of the river) in immense numbers early in March and remains about the rocks at the head of tide water for some time as though waiting for the coming shad or herring. With the shad they pass up the river beyond tide-water, and in the rapid rocky portions of the river having deposited their own ova, they wander over the breeding grounds of other fishes and devour every egg they can find. I have found lampreys in Crosswicks Creek in the month of May gathering up the eggs from sun fish nests." But here again the observation is not supported by an examination of stomach contents.

The only other observation known to me is that of Gage (1893) on *P. marinus unicolor*. "Of all the specimens obtained out of the breeding season either the digesting part of the alimentary canal was empty or it contained blood. No partly digested worms or insects or small fish or parts of fish flesh were found, although diligent search was made; consequently it is believed that the lake lamprey is wholly parasitic during its adult life and lives on blood sucked from other fishes." Again (p. 438) he speaks as follows of the intestine at the breeding season: "The atrophy takes place within two weeks, and begins at the terminal extremity, and extends gradually cephalad until the whole canal appears like a thread. As no food is taken during the spawning season there is no necessity for digestion, and in the female there is no room for the intestine when the ova are completely matured."

As it seemed incredible that the very elaborate rasping apparatus of this lamprey could have no other use than to enable the animal to produce a raw surface from which to suck blood, a thorough investigation of all the material of *P. marinus* at hand was made. But in all cases the intestines were found to be empty and atrophied. It was then learned that all the available lampreys had been caught in the breeding season. Through the kindness of Professors Gage and Wilder, however, I obtained several specimens of *Petromyzon marinus unicolor* taken in the breeding season and one specimen caught in December. The lampreys caught in the breeding season showed the same atrophied condition of the intestine that had been found in our own material, but the intestine of the one that was caught out of the breeding season was found to be gorged with food. The intestine measured 4 cm. in circumference while the intestine of a specimen of the same size caught in the breeding season measured but 6 mm. The œsophagus was entirely empty. Among the contents of the intestine solid particles could easily be seen with the unaided eye, while a microscopic investigation proved most of these to be muscular tissue. The more liquid parts were past recognition. There were recognizable bits of striated muscle about 12 mm. long, a gill and a rib of a small teleost fish. The gill was 1 cm. long and bore filaments 5 mm. in length; the rib was 2 cm. long. It is impossible to tell whether the lamprey came by this small fish directly or from the intestine of a larger fish which served as its prey.

In any case it appears that the attached *P. marinus unicolor* may feed not only on blood but on more solid tissue. The very extensive injuries produced by this species and figured by Surface (1893) are in accord with this conclusion. Presumably *P. marinus* and *Ichthyomyzon* have similar habits. According to Gage (1893) the adult *Lampetra wilderi* takes no food.

III. Mechanism of Respiration.

A. *When the Lamprey is Attached.* — Respiration may readily be studied when the lamprey is attached, and has been described by Bert (1867), Gage (1893) and Meyer (1835). The respiratory currents may be easily seen in *L. wilderi* and in *Ichthyomyzon concolor* by means of particles suspended in the water. There is a rapidly alternating contraction and expansion of the branchial region. At each contraction a current of water leaves all the external branchiopores simultaneously and passes outward and backward at an angle of 45° with the long axis of the body. At the same time a current issues from the nostril. With the expansion of the branchial region the water is seen entering the external branchiopores in lines converging from all directions to each aperture and at the same time a similar current enters the nasal opening.

Many factors vary the rate of the respiratory movements, such as the vitality of the individual animal, temperature and the oxygen content of the water.

The movement when the animal is attached is regular unless foreign particles get into the gills, in which case spasmodic contractions of the gills take place in order to expel the irritating particles. These contractions are essentially the same as in regular respiration except that they are longer continued and stronger, so that the external branchiopores are brought closer to the water tube. If many solid particles are suspended in the water the rate of breathing becomes slower and may even stop for a full minute, but if the animal is removed to clean water breathing again becomes normal.

During both expiration and inspiration the external branchiopores are wide open and look like so many gaping, round mouths. They do not change their form in either inspiration or expiration. The ectal valves are not taut; with the aid of a lens the ectal valves may be seen flapping idly back and forth in the opening (Fig. 10, *a*). With each inspiration the ental valves are seen to be swept back into the gill pouch much as swinging doors might be. At each expiration the out-flowing water sweeps the ental valves forward and out through the external gill opening past the loose border of the ectal valve (Fig. 10, *c*). It is thus clear that in the normal respiration of the attached lamprey the valves of the external branchiopores have no office other than to perhaps aid in directing the out-flowing water backward.

The movements of respiration and the working of the ental and ectal valves could be seen somewhat more plainly in *Ichthyomyzon concolor* than in *L. wilderi.* Besides the regular respiratory movements recorded for *L. wilderi* a slight backward and forward motion of the branchial basket was observed.

From the arrangement of the muscles of the gill sacs and gill pouches it may be inferred that the expulsion of the water is brought about by contraction in all directions of the lumen of the gill sac, while at the same time the long axis of the sac is more shortened than any of its other dimensions. Thus the capacity of the gill sac is reduced and a part of the water is expelled. The lateral end of the muscular pouch carries inward with it the elastic branchial basket to which it is attached. When the muscles relax, the elasticity of the branchial basket serves to elongate the gill sacs and thus to fill them again with water. The action may be likened to that of the mammalian lung in which the lung is filled by muscular action and emptied chiefly by the elasticity of the thoracic walls and lungs. The gill sacs of the lamprey are, on the other hand, filled by the elasticity of the branchial basket and emptied by muscular action. Not all the air in the lungs is changed by a single respiration and not all the water in the gill sacs can be changed at a single respiratory movement. The expulsion of the water at the angle of 45° does not retard but rather aids the progressive movement of the fish, while it permits the external branchiopores to have such a form and point in such a direction that they offer the minimum resistance to the movement of the animal through the water.

Gage's (1893) statement that the expired water leaves the external branchiopore at a very oblique angle with the long axis of the body while the inspired water enters at an angle of 90° suggests the possibility that during expiration the major axis of the gill sac forms a very oblique angle with the long axis of the body but that during inspiration this angle becomes a right angle. The following experiment was tried to find out whether there was any change in the obliquity of the gills during respiration: A bristle with as large a tip as would enter the external branchiopore was passed through the gill sac into the water tube so that it occupied the major axis of the gill sac. The end of the bristle was left projecting from the external gill opening and formed an angle of 45° with the long axis of the body. This angle remained constant during both inspiration and expiration.

Gage (1893, p. 469) believes this arrangement by which water leaves the gills at a very oblique angle while the inspired water enters at an angle of 90° is a contrivance to prevent the repeated respiration of the same water. The water does indeed leave the gill at a rather oblique angle (45°), but if the observations here made on the current entering the gill openings be correct, the water flows in from all directions much as it enters the mouth of an empty submerged bottle; moreover it is difficult to see the need of a contrivance to prevent the repeated inspiration of the same water. The expired water is thrown out with great force and to a considerable distance like a stream from a hose. It is thoroughly mixed with the adjacent water which by this means as well as by the movements of inspiration is kept constantly agitated. When we remember the rapidity with which gases diffuse through water thus agitated (Hoppe Seyler, 1896) there can be little doubt that the water inspired by a *Petromyzon* is of practically the same gaseous content as the adjacent water and is unaffected by the expired water. Probably a special contrivance for preventing the repeated inspiration of the same water is little more needed in *Petromyzon* than a similar contrivance for preventing the repeated inspiration of the same air in a mammal.

The current seen issuing from the nostril at each expiration is caused by the compression of the nasal cœcum. The caudal end of this cœcum is bounded above by the cephalic end of the notochord and below by the first two gill pouches (Fig. 1, *f*). As the gill sacs shorten with each expiration the cœcum is pressed against the notochord and water is forced from it. With the lengthening of the gill sac the walls of the cœcum are again separated and water is drawn into it. This current seems to have no other purpose than to bring the water in contact with the olfactory epithelium.

B. *Respiration when the Animal is not Attached.* — The acts of feeding and breathing have now been considered in the normal attached animal, and no use has been found for the velar valves, the velar jaws, the water tube or the valves of the external branchiopore.

When a gill sac expands there is created a negative pressure within it. To relieve this, water must enter the sac either through the internal branchiopore or through the external branchiopore or through both. When the animal is attached water enters necessarily through the external branchiopore alone. When the animal is not attached the mouth is open and water must enter through the external branchiopore, the valves of which are so constructed that they can offer no resistance to an inflowing current, but water may also conceivably enter the mouth, pass the velar valves and enter the gill sacs by way of the water tube and internal branchiopores. Thus both when the animal is attached and when it is not attached, water must enter the external branchiopores during inspiration. When the animal is not attached the water thus inspired through the external branchiopore may possibly be mixed in the gill sac with water inspired through the mouth. Indeed the inspiration of water through the mouth may be one means by which the unattached lamprey secures food. It is generally believed among writers (Mayer, 1835; Gage, 1893; Couvreur, 1897) that water may be inspired through the mouth of the lamprey when unattached. It is possible that breeding lampreys behave differently in this respect from those that are not breeding, but none of these authors state the time of the year in which their observations were made.

In order to ascertain whether water is normally inspired through the mouth, the following experiment was tried. A breeding *Lampetra wilderi* was placed in a wire basket which was in turn immersed in a dish of water. The meshes of the basket were small enough to keep the animal from getting out, but afforded no surface to which the animal could attach itself when it came to rest. A carmine mixture was placed near the mouth of the animal when it was thus quiet and unattached, but no current of water could be seen passing into the mouth. Many trials were made, but with the same result. This led me to the conclusion that in the adult lamprey, of this species at least, no current of water is taken into the mouth, but this is of course not true of the larval form.

On November 29, 1904, two living specimens of *Ichthyomyzon concolor* (Kirt), were obtained from the Detroit river and placed in a large aquarium. When one of these was placed on its back without unduly exciting it, the animal immediately became quiet and after a short time, while it remained in this position, could be handled as though it were dead. As soon as it assumed its normal position, however, the animal became active again. The phenomenon seemed to be of a hypnotic nature and obviated the necessity of giving chlorotone to quiet the animal.

While the animal lay on its back a mixture of carmine and water was poured into the upturned oral funnel. Now and again a red current of water could be seen passing into the mouth and out through the external branchiopores. After a few inhalations, the current would be reversed and a stream of water would be sent out of the mouth with some violence as though the carmine in the water was found to be irritating. The current of water passing into the mouth, it will be remembered, was not seen in the *L. wilderi*.

The two specimens were kept alive for five weeks in the laboratory when they died after being attacked by fungus. During their life in the aquarium, they were not observed to have taken any food, although large pieces of raw beef were suspended in the aquarium.

The only advantage to the lamprey of an inspired current through the mouth would lie in the fact that by means of such a current food might be caused to enter the mouth when the animal was free. The experiment on the inspiration of water through the mouth in *L. wilderi* above recorded was necessarily performed during the breeding season when the brook lamprey takes no food. It is therefore inconclusive. The similar experiment on *I. concolor* performed out of breeding season would tend to support the statement of Günther (1853) and Abbott (1875) that the lampreys feed when free as such feeding could hardly be accomplished without the inspired current through the mouth.

C. *Detachment and Regurgitation.*—The valves of the external branchiopores are clearly useless in aiding the animal to draw water into the mouth. There remains but one use for these structures, namely, to render possible an expired current through the mouth.

When the lamprey is firmly attached there is a partial vacuum in the mouth cavity and the oral hood. It would require considerable force for the animal to tear itself free when thus attached, but if by closing the external branchiopore and opening the velar valves and mouth it can force water into the oral funnel from the gill sacs, the vacuum will be at once destroyed and the animal may free itself without great muscular exertion. There is a further possible advantage to the animal in being able to expel a current of water from the gill sacs through the mouth. Such a current would enable it to cleanse the pharynx and mouth of indigestible and bulky food particles, nor does there appear to be any other means of accomplishing this.

In order to learn how the animal detaches itself the following observations were made : The ectal and ental valves of the external branchiopore were watched very closely with a lens to determine their action, if any, at the moment when the animal detached itself. This proved to be no easy task since the valves were found to act so quickly that one could see but a flash of white in the dark gill opening and the animal was gone before one could see what had happened. This difficulty was greatly lessened by the use of a small amount of chloretone in the water. This increased the rate of breathing at first but then gradually lowered it so that one could more easily tell what was taking place.

The cephalic and caudal sides of the gill opening were seen to be approximated so that instead of remaining circular, as during ordinary respiration the opening became elliptical with its longest axis dorso-ventral. Thus the ectal valve was stretched taut. The ental valves could be seen to come together so as to close this gill opening. Almost the instant the valves closed, the animal detached itself.

It thus appears that the valves of the external branchiopore, act in the manner indicated by their structure, to close the branchiopore at the moment when the animal detaches itself. Experiments were now tried to see if the water was sent to the mouth cavity to destroy the vacuum as it seemed from a knowledge of the workings of the valves and their action at the moment of detachment of the animal that it might be.

Experiment 1.—The head of a lamprey while attached to the side of a glass dish was gently pushed up out of the water without detaching the animal. Care was taken to thoroughly dry the the glass around the oral funnel. When the animal detached itself, water was seen to run down the side of the dish from the mouth.

If the lamprey's head and several gills were thus lifted above the water, air bubbles and water are expelled from the mouth upon the animals detaching itself. The air bubbles must have been taken in through the gill openings which were above the water and must have passed forward through the water tube and pharynx into the oral funnel.

Experiment 2.—A thin mixture of carmine and water was introduced into a gill of a *L. wilderi* attached to the side of a glass dish, by placing the end of a pipette over the external branchiopore and gently but steadily pressing the bulb. The animal expelled the carmine from the gill opening with violence. When a thicker mixture was used, the animal made a great effort to expel it, but when the carmine was still steadily poured into the gill, the animal detached itself and a stream of red was seen to issue from the mouth. When carmine was seen to issue from the mouth, no carmine issued from the gills, thus showing that the valves were acting to close the external branchiopore and to cause the water to take a forward course so as to make detachment easier for the lamprey. These experiments seem to leave no doubt that detachment is effected in *Lampetra wilderi* by a current of water forced from the gill sacs into the mouth cavity and that this is rendered possible by the closure of the external branchiopore by its valves.

As far as I have been able to find, the valves of the external branchiopore are mentioned by but two writers.

Mayer (1835) speaks of two flaps at the external branchiopore and describes them as being swept out and in through the branchiopore by the respiratory current. He assigns no function to them except that of forming a tube for the outflowing water.

Gage (1893) says: "In the case of the lamprey one might think at first that no valves were necessary in respiration, for if the branchial pouches are open to the surrounding medium through the branchiopores any enlargement of the branchial spaces would cause the water to enter, and conversely, any constriction would empty the branchial sacs. This view is correct but this mode of simply drawing water into a sac and expelling it has not apparently answered the requirements of the lamprey, and there is present the thin valve (the ectal valve) which covers the entire branchiopore in the larva, and in addition a double valve (ental valve), which is formed by the growth and modification of the middle gill lamella of the caudal half of the branchial sac." Concerning the function of the valves he says: "In inspiration the two parts of the inner or ental valve turn away from each other and are pressed toward the cephalic wall of the branchiopore across the channel at the edge of the branchial sac, and the ectal or transverse valve folds over the ental one. By the expansion of the branchial apparatus, the entrance to the gill sac has been rendered more direct and the inflowing stream flows directly into the sac. In inspiration, the water flows through the branchial lamellæ, while around the edges, *i. e.*, at the dorsal and ventro-lateral edges of the gill sac there is formed a canal or gutter by the shortening of the gill lamellæ. The free ends of the lamellæ are also membraneous and curved and aid in making a very complete and smooth canal. The ental valves at the entrance to the branchiopore cross this canal and serve as a guide to the inspiratory stream, not allowing the water to get into the canal around the edges of the gill sac, but directing it into the gill sac itself. In expiration, however, with the change in obliquity and the constriction of the gill sac, the water passes between the branchial lamellæ into the canal and meeting the ental valve rotates the two folds of the valves toward each other and against the caudal wall of the branchiopore, thus removing the obstruction in the canal and really extending it by means of the arched valves. From this arrangement it is seen that two distinct objects are attained, the water not only bathes the gills, but passes between the lamellæ, it is then concentrated in a canal with smooth sides where the friction is at a minimum and in its exit from the branchial sac in expiration the valves prevent the used water from making a circle in the gills, and more important, they form a very oblique channel which directs the expiring stream caudad, thus insuring the animal against using the water over and over. In inspiration, on the other hand, from the direction of the opening, the water enters at nearly a right angle to the axis of the animal, and thus fresh or unrespired water is constantly supplied to the gills."

It has been shown above that these valves have another function than the one indicated by Gage. That they may also act to direct the current of water within the gill sac as Gage believes, does not seem to the writer necessarily to follow from the observations on record. The course that water may take within the continuous space of the gill sac, during the inspiration and expiration seems to be determinable only by direct observation or by experiment, the inflowing stream may indeed be directed toward the center of the gill sac by the ental valve, but when the gill sac begins to empty itself the ental valves respond to the slightest current, the branchiopore is unobstructed and all the water within the gill sac is equally free to pass out through it. It would seem that the water should then flow directly out through the branchiopore rather than that it should take the circuitous course between the gill lamellæ into the smooth channel along the dorsal and ventral borders of the gill sac and thence out.

D. *The Velar Jaws.* — Mayer (37) gives a figure in which the velar jaws are shown, but gives no description of them.

Stannius (1840) speaks of thread-like projections from the cartilage of the velar valves and may thus possibly refer to the velar jaws.

Vogt and Yung (1889) described the velar jaws as a straining apparatus. From the cartilages of the valves "extend five long thin forked points directed forward with their converging ends and thus a strainer is formed which opposes the entrance of bodies from the pharynx."

I have examined the velar jaws of many specimens of *P. marinus* but have never seen them with projections or otherwise than smooth. That the jaws would act as a strainer and serve to hinder the entrance of foreign bodies into the water tube is clear from their position. From the fact that they close when the velar valves close, it is clear that they may seize and hold foreign bodies which are being carried into the water tube. If the velar valves should then open to permit the forward current from the water tube to enter the pharynx, the velar jaws would be opened by the same muscular contraction, the foreign body would be released and swept forward out of the mouth.

Nevertheless pending the examination of stomach contents the question as to what extent, if at all, the lamprey takes food by means of a current of water entering the mouth must be regarded as still open. If food is thus taken, it is quite possible that as food particles are swept past the velar jaws into the water tube the jaws may seize the larger particles, permitting the smaller ones to pass on with the inspired water. The closure of the jaws would be accompanied by the closure of the velar valves and the stoppage of the inflowing stream of water. If the velar valves were then opened, the jaws would open and the food would be released and if at the same time the œsophagus should open by relaxation of the posterior pharyngeus muscle, the jaws lie so near the opening of the œsophagus that the food with a small quantity of water would be swept into the œsophagus. The more one considers the mechanism, the more does the conviction deepen that the lamprey is able to feed by means of a water current through the mouth and by the aid of the velar jaw.

Summary.

1. When *Lampetra wilderi* is swimming, the sides of the oral funnel are approximated so that the opening into it is reduced to a narrow vertical slit, fringed by the oral cirri. The compressed oral funnel then serves as a vertical wedge-shaped cut-water.

2. When *Lampetra wilderi* is about to attach itself to any surface, the oral funnel is spread and applied to the surface with a quick backward and forward movement of the tongue and the animal becomes attached.

3. If an opening is made between the pharyngeal cavity and the exterior in *Lampetra wilderi*, the animal is still able to attach itself in the same manner as though uninjured.

4. If a communication be established between the mouth cavity or cavity of the oral funnel and the pharyngeal cavity or the exterior, the animal is unable to attach itself.

5. Attachment in *Lampetra wilderi* is therefore effected by means of a partial vacuum created in the cavities of the oral funnel and mouth by piston-like action of the tongue.

6. A dead *Lampetra wilderi* becomes firmly attached when its oral funnel is pressed against a surface with the fingers, and remains thus attached.

7. It follows from six that an attached *Lampetra wilderi* does not necessarily exert muscular energy to maintain its hold.

8. The oral funnel of a dead or living *Lampetra wilderi* may be moved about freely and very easily over the surface to which it is attached so that the animal is enabled to glide over the surface of its host and so change its position with ease.

9. The oral funnel of a dead or living *Lampetra wilderi* may

be pulled at right angles from the surface to which it is attached only by the exertion of considerable force.

10. It follows from 9 that *Lampetra wilderi* attached in a current of water may retain its hold without necessarily exerting muscular energy.

11. In inspiration in the attached *Lampetra wilderi*, water enters each external branchiopore and the nasal tube, coming gently from all directions, just as it enters the mouth of an empty, submerged bottle. It does not enter merely at an angle of 90° to the long axis of the body as stated by Gage for *Petromyzon unicolor*.

12. In expiration water leaves each external branchiopore in a backwardly directed stream which forms an angle of 45° with the long axis of the body. At the same time a stream issues from the nasal sac.

13. No muscular mechanism has been found to account for the expansion of the gill sacs by means of which inspiration is effected and the inpiration is therefore attributable to the elasticity of the cartilaginous branchial basket.

14. During expiration the gill sacs are compressed and their long axis shortened by the action of the following muscles: *a*, the internal and external compressors of the gill sac; *b*, the superficial compressors of the gill pouch (a muscular pouch which encloses each gill sac and is separated from it only by a large lymph space).

15. Water is forced out of the nasal opening at each expiration by the compression of the nasal cœcum between the notochord and the adjacent first and second gill pouches.

16. Water is drawn into the nasal opening at each inspiration by the expansion of the nasal cœcum due to its attachment to the adjacent medial walls of the second and third gill pouches which are separated by the elongation of the axis of these pouches during inspiration.

17. During both inspiration and expiration the external branchiopore has approximately circular form and the valves guarding it (ectal and ental valves of Gage) are seen to flap idly in and out of the opening.

18. The ectal valves may, as claimed by Gage, help to direct the inflowing current of water to the central part of the gill sac,

but the writer has obtained no evidence that this is the case, nor does she see any reason to believe that during expiration there is a movement of the water within the gill sac in the definite manner indicated by Gage.

19. In the attached *Lampetra wilderi* and *Ichthyomyzon concolor* in normal respiration, the ectal valve of Gage is relaxed, that is, its free edge is not stretched and no other function is observable in it than that of aiding in directing the expired current of water.

20. At the moment when *Lampetra wilderi* or *Ichthyomyzon concolor* detaches itself the dorso-ventral axis of the external branchiopores is seen to elongate so that the free border of the ectal valve is stretched taut. The ental valve at the same time strikes against the inner surface of the ectal valve and is thus prevented from turning outward. The external branchiopore is thus closed.

21. The elongation of the dorso-ventral axis of the external branchiopore is due to the contraction of the muscles, the ectal and ental, which act upon the cartilaginous ring to which the valves are attached.

22. If the head of a *Lampetra wilderi* is above the surface of the water, at the moment of detachment, a few drops of water are seen to issue from the oral funnel. If the head of an attached lamprey is far enough above the surface of the water so that two or more branchiopores are exposed, air and water issue from the mouth when the animal detaches itself. If carmine laden water has been introduced into the gill sac of an attached animal the head of which is submerged, a red stream is seen to issue from the mouth at the moment of detachment.

23. It is concluded from 20, 21 and 22, that detachment is effected by a current of water directed forward from the gill sacs through the water tube and pharynx so as to destroy the vacuum in the mouth and oral funnel.

24. If a thin mixture of carmine in water be introduced into the gill sac of a free *Lampetra wilderi* or *I. concolor* by means of a pipette held opposite the external branchiopores, the fluid is expelled from the external branchiopores by contraction of the gill sacs somewhat more violent than those of ordinary respiration.

25. If a thick carmine mixture be introduced as under 24 it

frequently happens that a violent contraction of the branchial region follows, accompanied by a discharge of the carmine from the mouth. At the moment of this discharge the external branchiopores are seen to be closed as noted under 20.

26. If a stream of thick carmine mixture be directed gently into the oral funnel of a free *Lampetra wilderi* or *Ichthyomyzon concolor* so as to fill the funnel, it frequently happens that there is a violent contraction of the branchial sac, accompanied by a stream of water which issues from the mouth and expels the carmine solution. At the same time the external branchiopores are seen to be closed as noted in 20.

27. It is concluded from 25 and 26 that a current of water from the gill sacs forward through the water tube, pharynx and mouth cavities is the agent by means of which these lampreys habitually cleanse pharyngeal and mouth cavities and is the only means by which bodies too large to pass into the alimentary canal or through the branchiopores, may be removed.

28. The current of water directed forward through the mouth, by means of which these lampreys are able to detach themselves and to cleanse the mouth cavity and pharyngeal cavity affords the first adequate explanation of the function of the valves of the external branchiopore, of the water tube and of the velar valve.

29. In the free *Ichthyomyzon concolor*, by the use of carmine and water, a gentle current may sometimes be seen entering the mouth during the inspiration and passing out through the gills.

30. The teeth of the oral funnel of *Petromyzon marinus* are so arranged in concentric loops that when moved in radial lines by the action of the annularis muscle they lacerate every part of the surface with which the funnel is in contact.

31. The tongue of the attached *Lampetra wilderi* or *Ichthyomyzon concolor* may be thrust forward so as to bring its teeth in contact with the surface of its host and thus when the animal is feeding the lingual teeth aid those of the oral funnel in lacerating the tissue of the host.

32. When the tongue is thrust forward in these attached lampreys so that it no longer serves to maintain the vacuum in the mouth cavity by closing the cavity posteriorly, the semiannularis muscle is believed to contract and thus to maintain the closure

of the mouth cavity. In this way the lamprey is enabled to use the tongue in feeding without loosening its hold on its host.

33. After relaxation of the semiannularis muscle the food in the oral hood of the attached lamprey is believed to be pumped into the pharynx by the piston-like action of the tongue working in the mouth cavity and to be forced thence into the œsophagus by the contraction of the muscles of the pharyngeal wall.

34. The intestine of a single specimen of *Petromyzon marinus unicolor* taken in December from Cayuga Lake, N. Y., was found to contain not only blood but muscle, bone, the gill arch of a small teleost and other tissues, probably those of the host to which the animal had been attached. Gage's ('93) statement that this species feeds only on blood of the host is thus erroneous.

35. In *P. marinus*, *Lampetra wilderi*, and *Ichyomyzon concolor* there projects forward into the pharynx from the cephalic end of the united walls of the œsophagus and water tube a pair of jaw-like structures, the velar jaws.

36. The velar jaws are adjacent to the velar valves which guard the opening from the pharynx into the water tube and the two are supported by a continuous pincer-shaped cartilaginous frame work, actuated by muscles in such a way that closure of the velar valves approximates the velar jaws; while opening of the velar valves separates the velar jaws.

37. When the attached lamprey is feeding, the velar valves close the entrance of the water tube and thus prevent food from entering the water tube and gill sacs. The velar jaws are closed and it is believed passive during this process.

38. The statement made by Günther (1853) and Abbott (1875) to the effect that the *free* lamprey feeds on fish and eggs or small invertebrates are not supported by the examination of stomach contents.

39. It may be possible for the lamprey to feed when free on minute forms or on somewhat larger animals siezed and held between the approximated halves of the oral funnel. The minute forms or the fragments resulting from the laceration of the larger forms might then be carried to the pharynx by a current of water entering the mouth.

40. If the lamprey feeds when free by means of a current of water entering the mouth it is possible that by a simultaneous closure of velar valves and velar jaws, food particles which would otherwise be swept into the water tube are held between the velar jaws. By the simultaneous opening of the velar valves and velar jaws a current of water from the mouth cavity into the pharynx might carry a food particle from the velar jaws into the open œsophagus. On the other hand, a current of water from the water tube might expel such a food particle through the mouth.

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